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Annual rhythms that underlie phenology: biological time-keeping meets environmental change

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Abstract

Seasonal recurrence of biological processes (phenology) and its relationship to environmental change is recognized as being of key scientific and public concern, but its current study largely overlooks the extent to which phenology is based on biological time-keeping mechanisms. We highlight the relevance of physiological and neurobiological regulation for organisms' responsiveness to environmental conditions. Focussing on avian and mammalian examples, we describe circannual rhythmicity of reproduction, migration and hibernation and address responses of animals to photic and thermal conditions. Climate change and urbanization are urgent examples of anthropogenic influences that put biological timing systems under pressure. We furthermore propose that consideration of *Homo sapiens* as principally a "seasonal animal" can inspire new perspectives for understanding medical and psychological problems.

Keywords: circannual, global change, photoperiod, hibernation, migration, urbanization, reproduction

1. MECHANISMS OF ANNUAL TIMING

In a seasonal world, precise timing of annual processes like reproduction, migration, diapause or hibernation is essential for survival and reproductive success. Accordingly, organisms have adapted to align with the predictable, periodic changes that are caused by geophysical cycles [16, 17, 37]. Phenology, the seasonal timing of recurring biological processes, is the result of these complex, and species-specific, timing processes [37, 106]. Because of the particularly evident importance of understanding seasonal timing in the context of global warming, phenology is an increasingly active field of study [36, 106]. Organisms have different mechanisms underlying annual cycles, but generally combine internal time-keeping with information from external cues to prepare for predictable, annual changes in their environment. For instance, cycles of hibernation and migration are considered to be adaptations for coping with harsh environmental conditions like low temperatures and low food abundance. However, both processes are commonly based on internal rhythms and can be solely triggered by seasonal change in day length [50, 58]. This is illustrated in Figure 1 for migration of songbirds. At the time of year when wild conspecifics migrate, stonechats (*Saxicola torquata*) show migration-related behaviour in captivity (eg, migratory restlessness), using day length as an external calendar. Under natural conditions, the timing of migration and other seasonal processes is further fine-tuned by additional environmental factors [29, 41, 113]. Thus, although the ultimate cause for cycles of migration and hibernation are predictable, periodically harsh environmental conditions, natural selection has favoured mechanisms that allow organisms to anticipate these conditions by internal rhythms and by use of proximate cues [4, 60].

The use of internal time-keeping mechanisms differs among species and can range from short-term interval timers to sustained rhythms that continue even under constant experimental conditions (Fig. 2) [16, 30, 37]). In some long-lived animal and plant species, internal time-keeping regulates annual cycles to such extent that they recur with periodicities that are close to, but not identical to one year ("*circannual*" rhythms [2, 42, 73]). Under natural conditions, environmental cues provide temporal information and synchronize circannual rhythms. The most reliable cue (*Zeitgeber*) is the annual change in day length or "photoperiod" [16, 17, 37, 77]. Other fluctuations also provide information for the timing of annual processes, for example ambient temperature, rain, or food availability, but the relative importance of these differs between species and environments [17, 60]. In tropical environments with high environmental unpredictability, temperature and rainfall cues may

increase in importance [45], while in the Arctic the timing of snowmelt initiates the growing season and can influence timing of animal reproduction (e.g., [54, 98]).

Species vary in their reliance on external cues *versus* internal time-keeping. Those living in environments where day length information is limited seasonally (eg, at the equator, during polar solstices or in deep ocean) or have lifestyles that make day length unreliable or temporarily inaccessible (eg, during migration and hibernation), typically relie greatly on internal time-keeping [2, 41, 42, 73, 85]. Species at mid-latitude locations use photoperiod as the dominant source of temporal information. These examples were thought to fundamentally differ, but now are increasingly seen as based on common mechanisms that are modified in species-specific ways (e.g., [16, 19, 47, 80]). Here we present an overview of the mechanisms by which animals keep track of time to create annual phenologies, with an emphasis on birds and mammals and a focus on circannual clocks.

Circannual rhythms – Circannual cycles persist in the absence of any external time cues across a wide range of taxa [42]. For example, when kept under constant day length and temperature conditions, pupation of larvae of carpet beetles *Anthrenus verbasci* and germination in the marine dinoflagellate *Gonyaulax tamarensis* recur approximately once per year [37, 45]. Most endogenous circannual cycles measured so far have periods shorter than 365 days [113], but some are longer [87] (Fig. 2). Thus, under experimental conditions phases of circannual cycles drift progressively towards either earlier or later dates.

Circannual studies have focused on birds and mammals, whose annual cycle comprises several phases, including reproduction, moult, migration or hibernation [41, 42, 68, 83]. These phases involve substantial modifications of morphology, physiology and behaviour that must be precisely orchestrated and occur at the correct time of year [42, 83]. Circannual rhythms were first described for hibernation in ground squirrels [85], where they persist under diverse lighting and temperature regimes [84]. Hibernating mammals maintain robust circannual cycles of seasonal weight gain, due to increases in food intake, fattening and anabolism, and profound thermoregulatory changes. Subsequently species may hibernate for 5-8 months, during which core body temperature can fall to as low as -3°C. Hibernation is followed by an active season characterized by a brief spring breeding period of 2-3 weeks followed by a weight gain of 2-3 times their emergence weight [15, 72]. While circannual rhythms in hibernating ground squirrels drift under constant conditions, hibernation cycles in the wild are synchronized with the external year. Thus, although hibernators remain

sequestered within a hibernaculum for much of their life in the wild, to remain synchronized with the external year an environmental *Zeitgeber* sets their clock.

Circannual rhythms are also particularly evident in long-distance migratory birds, whose amazing mobility implies a need to keep track of time of year [41, 42, 87]. Because the photoperiodic conditions that the birds experience depend on the latitude where they are flying, day length provides only ambiguous calendar information. For example, transequatorial migrants experience long days during both summer and winter [4, 60], and local cues like temperature and rain are usually unrelated to conditions in far-away target areas. Migrants that winter in tropical regions nonetheless accurately time departure for migration towards their breeding grounds. Gwinner was the first to demonstrate that some species, like the willow warbler (*Phylloscopus trochilus*), show persistent, circannual rhythms of migratory restlessness and other annual processes for several years when kept under constant environmental conditions [43]. In various migrants cycles of fattening, moult and reproductive competence also persist under circannual conditions [41, 42, 53, 112]. Figure 2 shows circannual rhythms of four avian species. The garden warbler (*Sylvia borin*) and the Great knot (*Calidris tenuirostris*) are long-distance migrants and show particularly clear circannual cycles [9, 87]. The figure also illustrates that photoperiodic conditions under which circannual cycles can persist ranged from constant dim light to 10 to 18 daily light hours. Similarly robust circannual cycles occur in mammals like the golden-mantled ground squirrel (eg., [92]). In some other species the expression of circannual rhythms was restricted to a narrow range of permissive day lengths (eg, [29, 42]).

A third group of animals with well-described circannual rhythms are species living near the equator where the photoperiod is almost constant and annual *Zeitgeber* information has low amplitude. A well-documented example is African stonechats (*Saxicola torquata axillaris*) that under constant conditions express circannual rhythms of reproductive capacity and moult for up to 10 years. These cycles persisted even in hand-raised birds that never experienced photoperiodic change [41, 50]. Although the cues that entrain circannual rhythms in tropical animals are still elusive, subtle changes in photic conditions may be useful. For example, Hau et al. [46] have shown that spotted antbirds (*Hylophylax naevioides*) respond to changes in photoperiod of as little as 17 minutes. Goymann et al. [39] recently suggested that stonechats might use the equatorial drift in sunrise and sunset time ("equation of time") to synchronize the circannual rhythm of moult. Other tropical species may use non-photic *Zeitgebers* or possibly express free-running circannual cycles [48]. However, tropical species may also respond directly to favourable environmental conditions,

especially in regions where seasonality has poor predictability. For example, rainfall is considered to be a strong predictor of food abundance in some arid regions. In Galapagos finches the reproductive system remains quiescent for most of the year but develops rapidly once favourable conditions arise [45].

Photoperiodism – Photoperiodism, "the ability of organisms to assess and use the day length as an anticipatory cue to time seasonal events" [16, 77], is pervasive among plants and animals. While day length provides timing information around the year, its effects on annual cycles are particularly well-studied for reproduction. The day lengths that activate reproduction differ between species and reflect the times of year when crucial preparations occur. In resident birds at mid-latitudes, the vernal increase in day length triggers a cascade of physiological events along the hypothalamus-pituitary-gonadal axis [29]. In birds and mammals, when day length increases the reduction of melatonin action in the Pars tuberalis (PT) promotes thyrotrophin (TSH) production, resulting in up-regulation of deiodinase2 and down-regulation of deiodinase3 in the Tanycytes lining the third ventricle. These changes in both enzymes cause an increase of local availability of active thyroid hormone (T3) in the anterior hypothalamus which may stimulate gonadotropin-releasing hormone (GnRH) neurons to release gonadotropins [28, 57, 75]. Gonadotropins promote the development of the reproductive organs, whose recrudescence increases release of steroid hormones. These stimulate brain receptors promoting reproductive behaviours like song, territorial aggression and courtship displays [22, 97].

Photoperiodism differs between birds and mammals in the input pathways to the hypothalamus. Mammals have a single pathway to the PT, in which plasma melatonin plays an essential signalling role [68]. The PT is rich with melatonin receptors [48]. Melatonin codes for day length because it is excreted at night by the pineal gland, which in mammals seems to be solely driven by the circadian pacemaker in the hypothalamic suprachiasmatic nucleus (SCN). In birds, the PT also expresses a melatonin receptor [27], but melatonin is not critical for the response although it may modify it [40]. Pinealectomized birds still show a photoperiodic response, which is most likely driven by hypothalamic photoreceptors [69]. In addition and in contrast to mammals, the avian pineal is itself a self-sustained circadian oscillator that entrains to light (Fig. 3 [22]). The hypothalamic photoperiodic response of birds and mammals converges in the involvement of local thyroid hormone metabolism, triggered by thyroid stimulating hormone (thyrotrophinsubunit β; TSHβ) [28, 92]. Along

these pathways, photoperiodism activates reproductive function either directly or by synchronization of an underlying circannual rhythm.

Photoperiodic response mechanisms of circannual clocks – Circannual clocks need to be synchronized by an environmental *Zeitgeber*, which usually is photoperiod. Circannual rhythms of some birds and mammals respond so strongly to photoperiod that by accelerated change of day length, several annual cycles can be forced to occur within one year [29]. However, effects of photoperiod on circannual rhythms depend on *Zeitgeber* strength and on species [73]. In sheep, a strong photoperiodic stimulus (8 weeks of short photoperiod) resets the internal circannual clock to a spring state irrespective of the timing of its application [68]. In contrast, in other species the response to calendar information depends on the phase of the underlying circannual rhythm (e.g., [52, 73, 74]). In birds, reproductive activation is usually stimulated by increasing photoperiod, but most species do not retain breeding condition indefinitely under long day length [52]. The phenomenon, whereby reproductive condition is terminated on long photoperiods and often initially not even re-stimulated by constant light, has been termed "photo-refractoriness" [44], although birds certainly remain responsive to photoperiod, and shortening days accelerate post-breeding processes like moult. As indicated by their sustained circannual rhythms, some species regain reproductive competence spontaneously (Fig. 2), while others restore a subsequent responsiveness to long photoperiods only after exposure to short days. This requirement for short days has been termed the breaking of refractoriness, but could also be seen as an advance of the underlying circannual system which in some species is obligatory [40, 45, 83]. Hence, it is not excluded that photorefractoriness, in birds and in mammals, could depend on a similar circannual timing mechanism [17, 19, 80].

In some mammals circannual rhythms are so robust that photoperiodic synchronization may be absent [47] or require several years after shifting day length [25]. Most hibernators are cut off from photoperiodic cues while they overwinter in closed or snow-covered underground burrows where daylight does not penetrate. Thus, timing of the end of hibernation and the beginning of reproduction relies on the circannual clock, which however is synchronized during the active season (mostly spring and summer). Lee and Zucker [66] demonstrated a role of day length changes experienced by animals during summer in the annual entrainment of circannual rhythms of golden-mantled ground squirrels (*Citellus lateralis*). Ground squirrels that were held on naturally changing photoperiods were more synchronized within groups and had longer cycle lengths between body weight peaks

and estrus (closer to 365 days) than conspecifics kept under constant conditions. This effect was lessened when circadian systems were impaired by SCN-lesions. Sensitivity to changing day length must be acute for photoperiod to entrain circannual rhythms of some hibernators, such as arctic ground squirrels, *Urocitellus parryii*, which are active above ground from only early May to late July, but are nonetheless entrained by the *Zeitgeber* [111].

Temperature and other factors - Other environmental factors can either modulate the interpretation of photoperiod or directly affect seasonal transitions [106]. These include food [70, 96], social interactions [51], weather conditions [29] and especially ambient temperature [21]. In hibernating mammals, changes in temperature can advance phases within circannual rhythms. For example, transferring hibernating male golden-mantled ground squirrels from 4 to 30°C in mid-winter terminated torpor and advanced reproductive maturation. However, in the subsequent year timing was not advanced in warmed compared to control animals, suggesting that the underlying circannual pacemaker was not affected [6]. Field and captivity studies that compared timing between locations and years showed that high spring temperatures advanced the end of hibernation and the onset of reproduction in ground squirrels [18, 71, 78]. Because prolonged cold temperatures in spring delayed the autumn body mass peak, the circannual rhythm appeared to be phase-delayed by cold temperature [62]. Therefore, high spring temperatures probably have direct causal effects on the phenology of hibernating mammals, while involvement of the underlying circannual rhythm remains unclear.

Several studies of birds [95] and mammals suggest that environmental temperature can affect photoperiodic synchronization of annual rhythms. For example, cold exposure at short photoperiods facilitates testicular regression in hamsters [65] and prairie voles (*Microtus ochrogaster* [63, 64]), and winter pelage change in Siberian hamsters (*Phodopus sungorus*) [93]. Critical photoperiod for the autumn regression of testes size in Siberian hamsters was reduced by about 7 min per degree of increased ambient temperature [101, 102]. Under natural photoperiod this may translate to a one-week delay of testicular regression when temperature is 4 degrees higher. Temperature effects in small mammals are thought to be mediated through melatonin [65, 93, 103], and would thereby take place through modulation of the essential input signal to the annual hypothalamic timing mechanism. Based on neuroanatomical evidence in the prairie vole, Kriegsfeld et al. [63] suggest that lower temperatures may inhibit the release of GnRH by neurons located in a brain area that also contains temperature-sensitive neurons. Together, these results suggest

that environmental temperature may act on both the input signal and the target neurons of the photoperiodic timing mechanism, but the precise nature of such temperature effects remains elusive [21].

Further relevant factors for annual cycles relate to social interactions. Just like daily rhythms [10], annual rhythms regulate functions whose value often depends on interactions with conspecifics, ranging from temporal mating associations to colony or flock formation for reproduction and movement [51]. Many organisms thus synchronize their activities to those of conspecifics. Responses to social cues may be integrated with the use of other cues. For example, in Siberian hamsters social influences interacted with temperature and food in the seasonal regulation of reproduction [81, 82]. Interestingly, these effects were only observed at intermediate photoperiods, suggesting that in this species they only act around the equinox to form a relatively mild modification of the all-over photoperiodic response.

Molecular mechanisms - The molecular mechanisms underlying variation in animal phenology are still unknown. Because photoperiodism involves the measuring of day length, the circadian system is likely to be implicated. The molecular mechanism underlying the circadian clock in eukaryotes involves periodic gene expression, with RNA and protein products from these 'cycling' genes defining the clock by operating within molecular feedback loops to generate their own rhythms [34]. An appealing candidate for phenological variation is the circadian gene *clock* (but see [7]). Recently, Liedvogel et al. [67] and Caprioli et al. [20] reported an association between polymorphism in *clock* and breeding phenology in birds.

Clock and other circadian genes could function through interaction with melatonin. Melatonin affects the expression of circadian genes, at least in mammalian peripheral clocks [59]. The promoters of numerous circadian clock genes show E-box elements, responsive to the circadian transcription factors CLOCK and BMAL1. Melatonin was found to affect the expression of several E-box controlled genes [61]. Two additional transcription factors: *eyes absent* 3 (*eya*3) and *six homeobox* (*six*) participate in mammalian responses to day length by forming a transcriptional coactivator complex that may contribute to inducing TSHβ. *Eya*3 promoter presents three E-box elements, and its expression is directly controlled by melatonin [28]. However, a general relationship between photoperiodic timers and the circadian pacemaker is still controversial.

The processes of modulating reproductive transitions probably involve epigenetic molecular regulation that alters temporal and spatial patterns of gene expression. Epigenetic

imprinting, resulting from genome - environment interactions, can further affect the following generations. Although direct effects of epigenetic modulation on annual cycles are unknown, perinatal exposure to various photoperiods or temperatures influenced circadian, endocrine or thermoregulatory traits later in life that could be highly relevant for seasonal timing [8, 24, 33]. This suggests an urgent need for further study.

2. ANNUAL TIMING IN A CHANGING WORLD

The current, rapid global changes in climate and land-use are likely to impair the functionality of biological time-keeping that had been fine-tuned over evolutionary history. Changes in phenology have been among the earliest observed "footprints" of global change (e.g., [55, 86, 108]), and are particularly evident in association with climate change and urbanization.

Climate change - Clear shifts in phenology have been related to warming, which can alter seasonality by advancing or extending the growing season, or by uneven warming patterns across the year [26, 35, 86]. Shifting phenology is also related to other changes in climate, such as changes in snow-cover (e.g., [54]), or, in tropical and arid habitats, patterns of rainfall [56]. However, species differ in the rate at which they adjust their timing to altered conditions [99, 106]. In particular, organisms at different trophic levels are modifying their seasonal processes at different rates, which can lead to progressively mismatched seasonal timing between interacting species.

A classic example is mistimed reproduction of great tits (*Parus major*) in The Netherlands. Peak availability of caterpillars, the main food for great tit nestlings, is advancing rapidly in response to increasing spring temperature and earlier oak bud burst [107]. Great tits show phenotypic plasticity in the timing of egg-laying, which allows them to adjust to warmer springs. However, this plasticity is limited by the complex mechanisms of avian reproduction, so that their breeding season is progressively delayed with respect to the food peak [108]. Although evidence for large effects on recruitment rates and population density is still scarce, mismatched timing of reproduction has imposed energetic and fitness consequences, including reduced fledging rate, fledging mass and adult survival [88, 104].

Compared to sedentary species like great tits, long-distant migratory birds might be additionally constrained in their response to changing phenology [13]. Pied flycatchers (*Ficedula hypoleuca*) in a Dutch oak tree forest laid their eggs earlier in response to warming

spring temperatures, but did not advance reproduction rapidly enough to compensate for the advancement of the food peak [11]. Such inadequate responses to changing weather patterns were associated with local population declines of European flycatcher populations [12]. For these migrants, annual migration appeared to have slowed the advance of breeding phenology. Pied flycatchers winter in West Africa, where they cannot access information about phenology on the breeding grounds and instead relie on circannual rhythms and day length to initiate spring migration. Their endogenous timing program appears to prevent birds from returning in time to advance breeding in a warming climate and from taking advantage of extended breeding seasons [14, 49]. New techniques for tracking migrants support this proposition by revealing remarkable constancy of individual timing [1].

In the Arctic, hibernating mammals may incur particular difficulties because the timing of spring events is largely set through circannual mechanisms in the previous summer or autumn. Nonetheless, in some hibernators the timing of annual events responded to climate differences due to altitude [18], latitude [5], and local differences in seasonality. Sheriff et al. [98] report on a 6-year study of two populations (Atigun and Toolik) of free-living arctic ground squirrels that live only 20km apart. However, due to differences in winter precipitation and wind, Atigun becomes snow free approximately 26 days earlier than Toolik. Ground squirrels differed consistently in the timing of spring emergence, parturition and re-entry into hibernation between the two sites (Fig. 3). These differences were not correlated with differences in soil temperatures, but instead, were presumably related to snow-cover [98, 111].

In addition to mismatches between interacting species, climate change may also disrupt the interactions of individuals within a species. In the ground squirrel example above, recent evidence suggests that the response of males and females to earlier snowmelt differs (MJ Sheriff, pers. comm). Similarly, males of many migratory bird species have advanced spring arrival more substantially than females [100], and in geese, adults may moult at progressively different times than their young [105]. Clearly, we need to understand mismatches on the level of individuals and populations to fully appreciate effects of global warming and climate-induced disruptions between interacting trophic levels.

Urbanization - Another important anthropogenic process that promotes phenological change is the rapid increase of urban sprawl. Urbanization entails the commonly reported effect of "urban heat island" [3], i.e., an air temperature excess over that of surrounding rural areas. A well-studied feature is the buffering of cold winters and reduction of temperature variation

between seasons [94]. Although its consequences are still poorly understood, it might be the major cause for the generally advanced plant phenology in cities, at least at temperate latitudes [76]. However, changes in plant phenology depend on functional type: early spring bloomers and insect-pollinated plants seem to advance their phenology more in response to warmer springs than late spring bloomers or wind-dispersed species do [35].

In animals, evidence that urbanization can alter seasonal timing is mostly based on bird studies. Avian city-dwellers in temperate areas show earlier development of the reproductive system [79, 96] and an overall extended breeding season [23]. It is possible that these changes are due to the warmer micro-climate in urban areas since temperature can directly affect the time of egg-laying [95, 115]. However, urbanization could also alter phenology by changed photic conditions due to artificial lights at night. Light pollution could modify perceived day length through increased ambient illumination and/or shifts in spectral properties of light [89]. Recent experimental work demonstrated that light at night can substantially advance the reproductive physiology of European blackbirds (*Turdus merula*) [32]. The possible fitness consequences of such phenological changes in cities are still poorly understood.

Urbanization should be a rewarding model system for understanding phenological change. Two research directions could exploit the potential of an integration of urban ecology and chronobiology. The first is possible differences in cue sensitivity between urban and rural species, and in the response of internal systems of the circadian and circannual clock to urbanization pressure. The second direction is elucidation of the fitness consequences of modified phenology. For example, do birds and insects modify their phenology in cities at similar rates? And what are the consequences of potential mistiming on urban ecosystem function? Modification of seasonal rhythms might allow wild organisms to succeed in human cities, but for some species, it might equally be a lost race around the annual clock.

3. ANNUAL CYCLES IN A CHANGING WORLD – OF HUMAN CONCERN?

Two key processes of global change, climate change and urbanization, rapidly modify phenology and may impose substantial challenges on wild organisms, and consequently, on humans. However, because the observed patterns differ so widely, it is difficult to interpret and predict organisms' responses. In this review we have summarized the diversity and complexity of the mechanisms that underlie phenology. The control and expression of annual

cycles vary in the degree of flexibility depending on the species, on the environment where they live, and on the temporal cues that affect their physiological systems [36, 106]. The difficulties in explaining organismic responses may be largely due to our limited understanding of the diverse timing mechanisms, and specifically to a neglect of contributions by biological clocks. These difficulties can be jointly addressed by ecologists and chronobiologists [17, 37, 106].

In addition, the annual change in environmental conditions and the current changes in seasonality may affect humans in ways that are still more direct. We have a very limited understanding of the extent to which our own species is affected by and responds to seasonality [37, 38]. Until the recent past the changing seasons had markedly influenced human biology, with indication of annual cycles of reproduction, immune function, disease and death. Since then, humans have become progressively isolated from seasonal changes in temperature, food and photoperiod in the industrialised nations. Nevertheless, the seasons continue to have effects on our lives. An individual's birth, susceptibility to disease, and death are not randomly distributed across the year in modern societies [31, 39, 46]. It is difficult to explain why this seasonality still exists in the modern world, in particular as food availability is largely constant and seasonal changes in ambient temperature are largely abolished in industrialized societies [38]. A possible explanation is that these cycles are residuals of responses that had evolved originally in our ancestors, who - like other tropical species - may have timed physiological processes by circannual clocks and environmental cues. Perhaps we have retained a circannual timer that can be synchronized by photoperiod or metabolic status (eg, [42, 109, 110]). Alternatively, as our ancestors moved from Africa to the higher latitudes and encountered progressively greater variation in food availability and temperature, they could have evolved a strong photoperiodic response [58, 80].

Recent studies provide increasing support for the idea of humans as a "seasonal species" that responds to photoperiod. Human daily activity patterns are influenced by the solar day [91], and the specific timing of activity ("chronotype") differs between populations along latitudinal gradients [90]. Humans, along with other primates, have the basic biological machinery that would drive a response to seasonally changing light exposure [109]. Hence, some aspects of human seasonality may be explained by its effects. The reported effects of mammalian maternal light exposure on offspring further suggest that health and well-being, from brain function to endocrine status, may be indirectly influenced by photoperiod [8, 24, 33]. Figure 4 shows results from a recent meta-analysis of the occurrence of *anorexia nervosa* in British cohort studies [43]. Patients who suffered of *anorexia* were much more

likely to have been born in spring and much less likely to have been born in autumn than the general population. Such patterns, and increasingly more examples of seasonality in epidemiology, are still poorly understood. Possible contributions of circannual rhythms also cannot be excluded. These are difficult to test in humans but have been documented in other primates [109]. A case study of seasonal affective disorder reports suggestive data of a possible circannual rhythm from a single patient [114], which, if confirmed, could open new prospects for treatment. Regardless of the specific, underlying timing mechanism, an increasing number of studies indicates that a closer look at seasonal patterns in our own species could contribute to health and well-being.

4. OUTLOOK

Seasonal variation shapes the life-cycles of animals and plants, and their adaptations to such change play a large part in determining their survival and reproductive success. The same is true for humans. The difference is that we have developed and adapted in such a way that we survive environmental change by modifying the environment. But in modifying the world we have lost contact with nature and its timing, and feel ourselves immune from such changes. An understanding of phenology and the internal timing mechanisms in which we and other organisms have adapted to environmental change will help us both mitigate and manage some of the broad effects of seasonal change, including the impact of global climate change. It will provide evidence-based approaches for the development of new therapeutic, agricultural and horticultural practices, the means to protect human health from attacks by both old and resurgent pathogens, and strategies for the conservation of other species [37].

Figure Captions

Figure 1. Onset of migratory restlessness ("*Zugunruhe*") in relation to day length in captive stonechats. With later hatching date, birds developed under progressively shorter European day lengths, and accordingly prepared for autumn migration at progressively earlier ages. This was observed for European migratory stonechats (blue triangles, dashed line) but also for African resident stonechats (orange dots, solid line). Inlay: pairs of African (right) and European (left) stonechats (from [50]).

Figure 2. Circannual rhythms in birds. The figure shows four different species kept under a wide range of day length conditions: three songbirds (a to f) and one wader (g, h). For each species, data from two individuals were chosen as examples. Y-axis represents testis size (a to d), testis mass (e, f), or body mass (g, h), X-axis represents time in months. Vertical dashed lines mark transition between years. Black bars represent moulting periods. LL: constant dim light; LD: light-dark cycles of different duration.

Figure 3. Local differences of seasonal events in neighbouring populations of female arctic ground squirrels in Northern Alaska (68.5°N). Bars (mean ± SE) show consistently earlier timing at Atigun (blue bars), where snow-melt occurs substantially earlier, compared to Toolik (green bars). a) Resumption of euthermy in spring, b) emergence from hibernation and resumption of surface activity, c) parturition date, d) beginning of hibernation, e) initiation of heterothermy. Faded lines indicate lack of precise data.

Figure 4. Proportional distribution of *anorexia nervosa* in relation to month of birth. Curves show the percentage of births for a given month in patients suffering from anorexia (drawn out) compared to that of the general population (dashed). Based on [43] and reproduced with kind permission by the Royal College of Psychiatrists.

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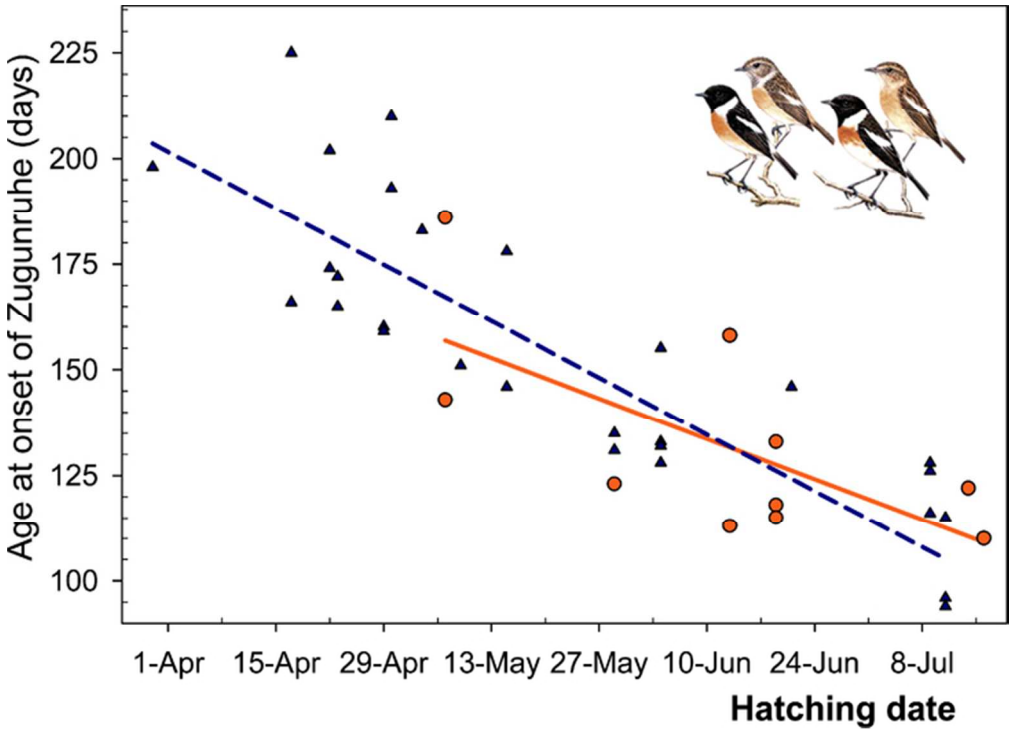

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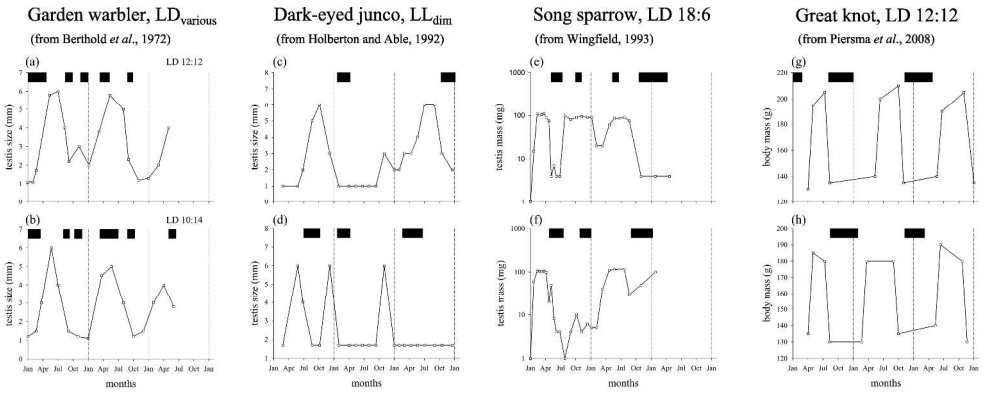
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(from Holberton and Able, 1992)
Song sparrow, LD 18:6
(from Wingfield, 1993)
Great knot, LD 12:12
(from Piersma et al., 2008)
(a)
LD 12:12
(b)
LD 10:14
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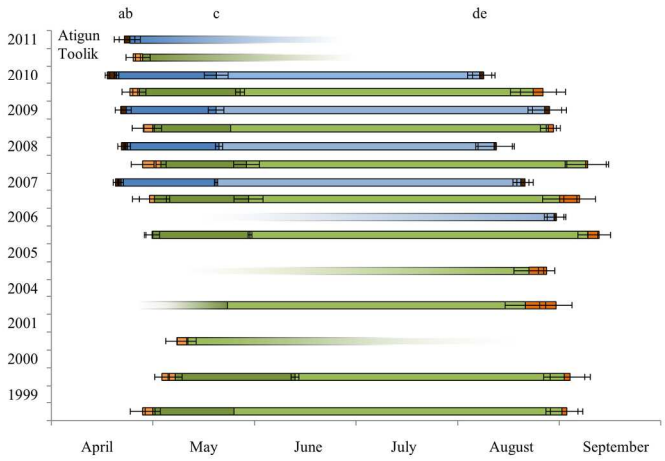

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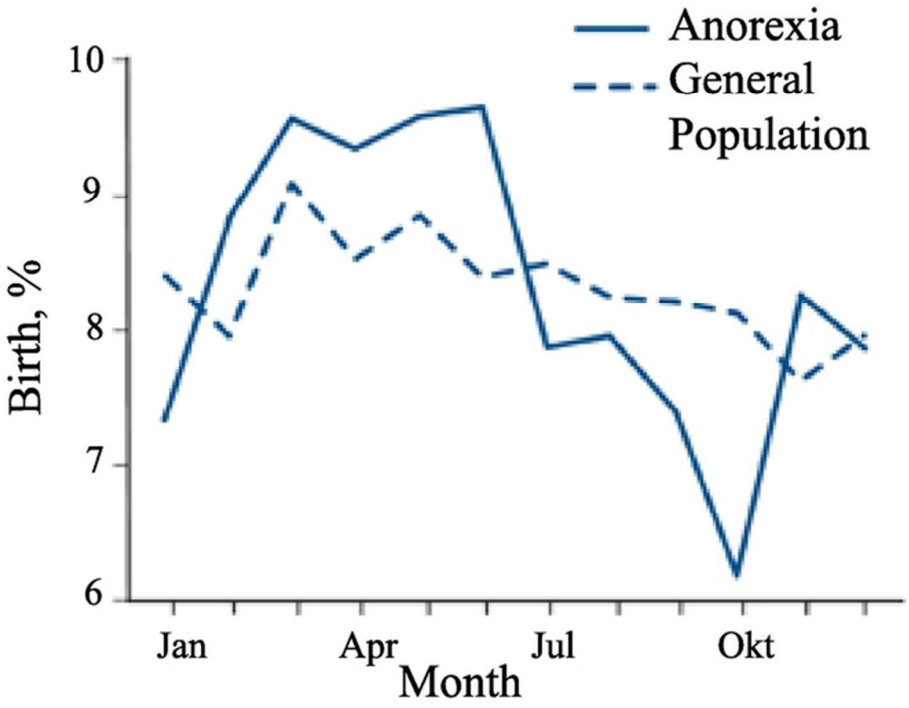

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